SPARTINA (GRAMINEAE) IN NORTHERN CALIFORNIA: DISTRIBUTION AND TAXONOMIC NOTES

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ABSTRACT

In addition to the native *Spartina foliosa,* four species of *Spartina* have been established in San Francisco Bay by human introduction. One species, *Spartina patens,* has been reported previously and appears to have been introduced accidentally. Three species, *S. alterniflora, S. anglica,* and *S. densiflora,* have been introduced in attempts to establish cordgrass within marsh restoration projects. Only *S. alterniflora* and *S. densiflora* have spread beyond their original sites of introduction. The latter species has been introduced from Humboldt Bay, where it was previously included in the taxon *S. foliosa.* Morphological and ecological data support the conclusion that the species occurring in Humboldt Bay should be referred to as *Spartina densiflora* and was probably introduced to northern California from South America during the mid-nineteenth century.

Mobberley (1956), in his monograph of the genus *Spartina,* cites two species in California: *Spartina foliosa* Trin., found in coastal salt marshes, and *Spartina gracilis* Trin., found along inland alkali lakes and streams. The distribution of *S. foliosa* is given as Baja California to Humboldt and Del Norte Counties by Mobberley (1956), Mason (1957), Munz (1973), and Macdonald and Barbour (1974), whereas Jepson (1925) and Hitchcock (1935) cite San Francisco Bay as being the northern limit. Since these accounts, new information has been gathered on the occurrence of this and several additional *Spartina* species in the salt marshes of northern California.

Coastal SPARTINA *in California. Spartina foliosa* (California cordgrass) is the dominant *Spartina* in southern and central California and San Francisco Bay. Its northern coastal limit occurs north of San Francisco Bay at Bodega Bay. The single patch (ca. 20 m × 30 m) suggests its presence there is recent. *Spartina foliosa* is also present at Bolinas Lagoon and Drakes Estero, but is absent at Tomales Bay even though suitable habitat seems to occur. Macdonald and Barbour (1974) note its "conspicuous absence" here and in several other estuaries and lagoons in California. No *Spartina* occurs north of Bodega Bay until Humboldt Bay and the nearby Eel River delta. In the past, *Spartina* at these two locations was regarded as an ecotype of *S. foliosa* (Mobberley 1956, Gerish 1979, Rogers 1981,

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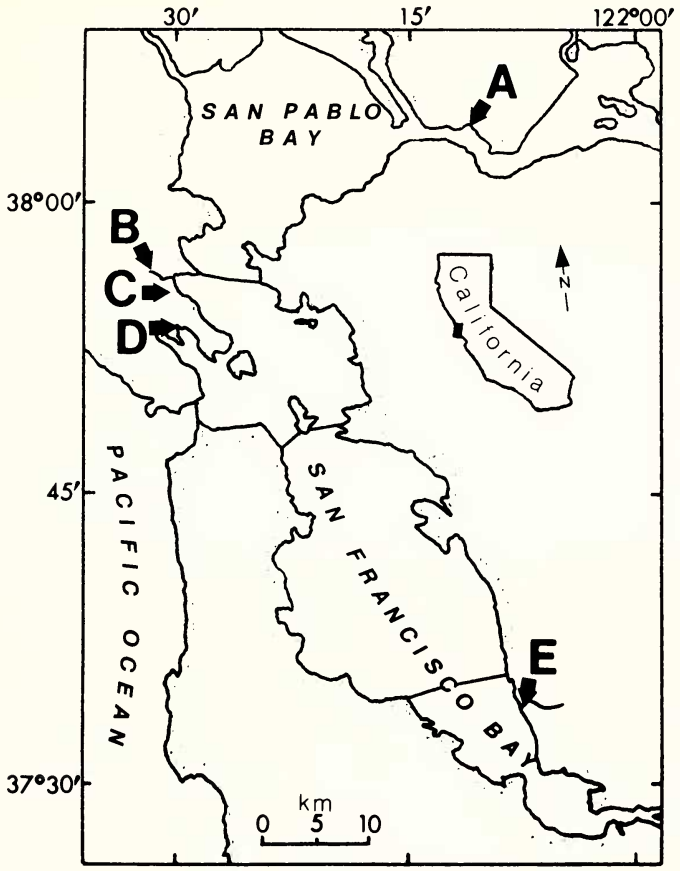

FIG. 1. Locations of introduced *Spartina* spp. in San Francisco Bay. A—Southampton Bay (*S. patens*); B—Creekside Park (*S. densiflora, S. anglica*) and Corte Madera Creek (*S. densiflora*); C—Muzzi Marsh (*S. densiflora*); D—Greenwood Cove (*S. densiflora*); E—Alameda Creek Flood Control Channel (*S. alterniflora*).

Claycomb 1983). However, as discussed in further detail below, ecological and taxonomic investigations have shown it to be a distinct species, *Spartina densiflora* Brong. Despite reports that *Spartina* occurs in Del Norte County (Mason 1957, Munz 1973), we have not seen it north of Humboldt Bay as far as and including Coos Bay, Oregon.

Introduced SPARTINA *in San Francisco Bay.* Until 1973, *Spartina foliosa* was the only *Spartina* described for San Francisco Bay. Since then, four more species have been introduced either accidentally or intentionally: *Spartina patens* (Ait.) Muhl., *Spartina alterniflora* Lois., *Spartina anglica* C. E. Hubbard, and *Spartina densiflora.*

FIG. 2. Introduced *Spartina alterniflora* near the mouth of the Alameda Creek Flood Control Channel. It is taller than *S. foliosa* which is in the foreground.

Munz (1973) reported *Spartina patens* (saltmeadow cordgrass) for Southampton Bay (A—Fig. 1). We found an existing patch, but this species does not appear to have spread from its original location. The second species, *S. alterniflora* (smooth cordgrass), occurs at the mouth of the Alameda Creek Flood Control Channel (E—Fig. 1; Fig. 2) and along the shoreline approximately 3 km to the south. Both of these species are endemic to salt marshes of the eastern United States. The method and precise date of their introduction into San Francisco Bay are unknown.

The third species, *Spartina anglica* (common cordgrass), was introduced at Creekside Park Marsh (B—Fig. 1) from Puget Sound, Washington in 1977 (K. Floyd, pers. comm.). These particular plants have been renamed internationally and misidentified locally in the past, so the use of *S. anglica* requires clarification. Locally in San Francisco Bay, they have been called *Spartina maritima* (K. Floyd, pers. comm., Hedgpeth 1980, Josselyn and Buchholz 1984). Taxonomic descriptions (Mobberley 1956, Hubbard 1968) and herbarium specimens [374220, 466912 (CAS)] clearly indicate these plants are not *S. maritima*; their oversized culms, leaves, and spikelets are among deciding features (Table 1) that place them in *S. anglica.* The name *S. anglica* was coined when two forms of *S. townsendii* (Townsend's cordgrass) were separated nomenclaturally. *Spartina townsendii,* discovered in England in 1870, was regarded as a sterile

TABLE 1. COMPARISON OF MORPHOLOGICAL CHARACTERISTICS BETWEEN *Spartina maritima* AND *S. anglica* AS DESCRIBED BY HUBBARD (1968) AND *S. anglica* FROM CREEKSIDE PARK MARSH, KENTFIELD, CA.

Feature	Species		
	S. maritima	*S. anglica*	*S. anglica* (Creekside Park)
Culms	to 50 cm tall	to 130 cm tall	to 126 cm tall
Blades	2–18 cm long to 6 mm wide	10–45 cm long 6–15 mm wide	36–46 cm long 11–13 mm wide
Ligules	0.2–0.6 mm long	2–3 mm long	to 2.5 mm long
Inflorescence	4–10 cm long	12–40 cm long	27–33 cm long
Spikes	1–5 in number	2–12 in number	8–11 in number
Spikelets	11–15 mm long	14–21 mm long	16–20 mm long
Anthers	4–6 mm long	8–13 mm long	8–10 mm long

hybrid resulting from the natural hybridization between the alien *S. alterniflora* from America and the endemic *S. maritima* (Hubbard 1968, Ranwell 1967, 1972). In 1892, a fertile form appeared, apparently a result of natural chromosome doubling (Hubbard 1968, Ranwell 1972). This fertile form remained unnamed until 1968, when Hubbard (1968) gave it the binomial, *Spartina anglica* C. E. Hubbard. The male-sterile hybrid is now *Spartina* × *townsendii* H. and J. Groves (Hubbard 1968).

Because of its aggressive colonization and effective sediment-accreting abilities, *Spartina anglica* (and perhaps *S.* × *townsendii*) ramets were distributed worldwide upon request for creating salt marshes and controlling shoreline erosion (Mobberley 1956, Ranwell 1972, Chung 1983). In 1961 or 1962, as H. M. Austenson noted on a specimen [M155990 (UC)], Washington State University and the U.S. Department of Agriculture introduced *S. townsendii* in Puget Sound, Washington (Snohomish County, Stillaguamish Estuary, near Stanwood). These plants are now known to be *S. anglica* because ramets of these plants introduced at Creekside Park Marsh flowered and produced 20% viable seeds in 1983. No flowering occurred in 1984.

Spartina densiflora (Humboldt cordgrass) is the fourth *Spartina* introduced in San Francisco Bay. As mentioned previously, this species was introduced at Creekside Park Marsh in 1977, and was thought to be an ecotype of *S. foliosa.* Its present distribution in San Francisco Bay is limited to Marin County: at Creekside Park Marsh and Corte Madera Creek, Muzzi Marsh, and Greenwood Cove (Fig. 1).

Taxonomy of the Humboldt Bay SPARTINA. In 1932, the identity of the *Spartina* growing in Humboldt Bay was questioned when Saint-Yves (1932) annotated a specimen identified earlier as *S. fo-*

TABLE 2. COMPARISON OF MORPHOLOGIC, PHENOLOGIC, AND ECOLOGIC CHARACTERISTICS BETWEEN *Spartina foliosa, S. densiflora* AT CREEKSIDE PARK MARSH, AND *S. densiflora* IN SOUTH AMERICA AS DESCRIBED BY MOBBERLEY (1956). Information for *S. foliosa* is from Mobberley (1956), except where noted, and for *S. densiflora* in Creekside Park from Spicher (1984). [a]—Kasapligil (1976), [b]—Spicher (1984).

	Species		
Feature	*S. foliosa*	*S. densiflora* (Creekside Park)	*S. densiflora* (Mobberley 1956)
Culms	to 1.5 m tall (to 2 m)[a]	to 1.4 m tall	to 1.5 m tall
	fleshy	indurate	indurate
	evenly spaced from rhizomes	caespitose from knotty bases	caespitose from knotty bases
Blades	flat to loosely involute	involute	involute
	8–12 mm wide[a]	6–7 mm wide	3–8 mm wide
	adaxial surface glabrous	adaxial surface scabrous	adaxial surface scabrous
	abaxial surface glabrous	abaxial surface glabrous	abaxial surface glabrous
	36–50 blade ridges[a]	9–10 blade ridges	—
Inflorescence	12–25 cm long	8–23 cm long	10–30 cm long
	—	5–10 mm wide	4–8 mm wide
Spikes	4–10[a]	6–20	2–15
	2–8 cm long	1–5.5 cm long	1–11 cm long
Spikelets	8–30	5–27	10–30
	8–25 mm long	9–12 mm long	8–14 mm long
Flowering period	July to November	April to July	—
Seed set	October–November[b]	August	—
Habitat elevation	1.1–2.7 feet (NGVD)[b]	2.0–3.6 feet (NGVD)	—

FIG. 3. Individual tussocks of *Spartina densiflora* at Creekside Park Marsh occupy slightly higher elevations (A) while *Spartina foliosa* forms meadow-like stands nearer channels (B).

liosa by Hitchcock to be *Spartina densiflora* Brong. forma *acuta* St. Y. Mobberley (1956) rejected Saint-Yves' reidentification, stating that Saint-Yves based his decision only on the smaller spikelet lengths of the Humboldt Bay species. However, Saint-Yves (1932) based his opinion on three features: difference in spikelet lengths, difference in foliar structure, and strongly keeled glumes in the Humboldt Bay *Spartina.*

Mobberley (1956) subdivided *Spartina* into three species complexes. The first contains species with numerous short, closely imbricate spikes, hard slender culms, and short (or even lacking) rhizomes (e.g., *S. spartinae*). Complex two is characterized by species with thick, succulent, fleshy culms that grow from solitary bases or in small clumps; spikelets are usually less closely imbricate. These plants rarely show purple coloration (e.g., *S. foliosa*). The third complex contains species with indurate culms, more or less spreading spikes with closely imbricate spikelets, and very often are streaked or tinted with purple color. *Spartina patens* and *S. densiflora* are members of this group.

A comparison of some morphological, phenological, and ecological characters of the Humboldt Bay *Spartina* with those of *S. foliosa* and *S. densiflora* were made from living and herbarium specimens (Table 2). The caespitose habit of the Humboldt *Spartina,* which

differs from the solitary, evenly-spaced culms of *S. foliosa,* is the most visible difference between the two species (Fig. 3). The Humboldt Bay *Spartina* possesses all the characteristics of Mobberley's third complex (*S. densiflora*) except for its usually appressed-imbricate spikes. Mobberley (1956) amends his general rule for *S. densiflora,* however, which possesses appressed spikes.

There was speculation that the *Spartina* in Humboldt Bay was *S. spartinae* (Gerish 1979). *Spartina densiflora* does share some characteristics with *S. spartinae,* but Mobberley (1956) distinguished *S. densiflora* and *S. spartinae* in South America as follows:

1) spikelets of *S. densiflora* exceed 8 mm, whereas those of *S. spartinae* do not exceed 7 mm (some N. American specimens to 10 mm)
2) trichomes of *S. densiflora* are short, rigid, and slender; they are about one-half as long as the thicker trichomes of *S. spartinae*
3) the first glume of *S. densiflora* is about one-half as long as the second; rarely is the first shorter by more than 2 mm in any of the other *Spartina* spp., including *S. spartinae*

The differences between herbarium specimens (CAS, UC) (Table 3) of *Spartina spartinae* and *S. densiflora* were found generally to be true. Not all characteristics are necessarily found in every spikelet, but the smaller spikelets and longer, thicker trichomes on the spikelets of the *S. spartinae* inflorescence give it a tighter and more pubescent appearance than in the inflorescence of *S. densiflora.* The spikelets and inflorescences of the Humboldt Bay *Spartina* closely resemble those of *S. densiflora.*

Gerish (1979) found the chromosome number of the Humboldt Bay *Spartina* to be $2n = 60$, the same number counted for *S. foliosa* by Parnell (1976). Gerish inferred that the Humboldt Bay *Spartina* was from *S. foliosa* genetic stock and that any morphological differences were caused by genotypic or phenotypic processes. Although the chromosome numbers match, this single common denominator does not demonstrate conclusively that they are the same species. Many species in the genus have identical chromosome numbers (Moore 1973, Goldblatt 1981).

SPARTINA DENSIFLORA *introduction to North America. Spartina densiflora* is almost certainly not native to Humboldt Bay. Its distribution was reported previously only in South America below the 23rd parallel (Mobberley 1956). If it were a North American native, it would be expected to occur more extensively than in just one location.

Therefore, *Spartina densiflora* was probably introduced into Humboldt Bay, as were many organisms in other estuaries of Cal-

TABLE 3. IDENTIFICATION NUMBERS OF HERBARIUM SPECIMENS STUDIED IN COMPARING THREE *Spartina* SPECIES AT THE UNIVERSITY OF CALIFORNIA HERBARIUM, BERKELEY AND AT THE CALIFORNIA ACADEMY OF SCIENCES, SAN FRANCISCO. Locations where specimens were collected are abbreviated in parentheses [California (CA), Texas (TX), Louisiana (LA), Florida (FL), Mexico (MX), Brazil (BR), Uruguay (UR), Argentina (AR), Costa Rica (CR)].

Herbarium location	Specimen identification number		
	Spartina foliosa Trin.	*Spartina densiflora* Brong.	*Spartina spartinae* Trin.
UC Berkeley	M260502 (CA)	298388 (UR)	M153237 (TX)
		MO47062 (BR)	821629 (TX)
		MO27317 (BR)	35760 (MX)
		627472 (AR)	
		627546 (AR)	
		MO25678 (UR)	
California Academy of Sciences	444653 (MX)	101351 (AR)	303562 (CR)
	368772 (CA)		686493 (MX)
	440197 (CA)		382866 (FL)
	386343 (CA)		182083 (LA)
	418931 (CA)		
	274331 (CA)		
	101332 (CA)		

ifornia in modern times. In San Francisco Bay after 1850 for example, organisms were introduced unintentionally by ships from foreign lands. Among these organisms were many marsh plant species, including *Atriplex semibaccata* (L.) Presl. (Australia) and *Cotula coronopifolia* L. (South Africa) (Munz 1973, Atwater et al. 1979).

Similarly, *Spartina densiflora* may have been introduced from Chile. During the 1850s and early 1860s, Chile experienced a period of rapid economic growth that created a demand for processed lumber, much of which was supplied from the northern California coast and Humboldt Bay (Cox 1974, Carranco 1982). Many company-owned lumber ships returned from South America without heavy cargo. For stabilization these ships often took on solid ballast gathered from the shoreline. The Chilean beachhopper, *Orchestia chiliensis,* was introduced to San Francisco Bay in this manner, by the "Discharge of shingle ballast (stones, algae, and debris gathered from beaches) by lumber ships returning from Chile in or before 1900 . . ." (Carlton 1975). Similarly, we propose that seeds of *S. densiflora* were brought to Humboldt Bay from Chile. Spicher (1984) showed that the seeds of this species are tolerant of long periods of storage in either dry or moist conditions. In addition, Mobberley (1956) found *S. densiflora* spikes to shorten in length and increase in number on inflorescences of plants from north to south along the east coast of South America and across to Chile. The greater number

and shorter spikes of the Humboldt Bay *Spartina* (Table 2) reflect what might be expected in *S. densiflora* from Chile.

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